Weismann (Aug)

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TRANSLATED BY HENRY M. DOUGLASS.

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ON THE CHANGE OF THE MEXICAN AXOLOTL TO AN AMBLYSTOMA.

By Dr. August Weismann, *Professor at Freiburg, Breisgau.*
[Translated by Henry M. Douglass, Champaign, Ill.]

Since Duméril first announced the change of a number of Axolotls into the so-called Amblystoma form, this Mexican fish-salamander has been bred in aquariums at many European places, principally with a view to determine the conditions under which that change occurs, and then from that to draw further conclusions upon the real causes of this exceptional and therefore so mysterious metamorphosis.

The creatures were easily propagated everywhere, and that in great numbers. Yet not only did the cases in which the transformation occurred remain exceedingly rare, but no one succeeded in answering the first and most important question, whether this was called forth by *external* circumstances or was dependent upon purely intrinsic causes. Much less were any *definite* external influences found through whose presence one could bring on the metamorphosis with certainty.

But until this point is decided, all attempts at theoretical interpretation and use of the phenomenon must remain without any firm foundation.

To me this history of the Axolotl's transformation always seemed to be of quite a particular interest. I believed, indeed, that possibly this *one* special case might be sufficient to determine the correctness of the fundamental principles, according to which the origin of species is represented in the two hostile camps of *development* and *heterogeneous* or *distinct* creation. So I resolved to set about experiments with the Axolotl myself, in the hope that perhaps it would be my good fortune to throw some light upon this subject.

In the year 1872, Herr von Kölliker had the kindness to present to me five of the Axolotls he had bred in Würzburg. In the following year these produced an abundant brood. With them I tried to settle the question, whether it was not possible to force all the larvæ to the change, or at least the greater part, if they were brought into circumstances which rendered the use of the gills difficult, that of the lungs easy. This, in other words, would be to compel them from a certain age to live half on the land. It will be seen further on, what theoretical grounds led me to this idea.

Meanwhile I reached no results that year. The most of the larvæ died before the time for such experiments seemed to have come. The

few survivors did not make the change, but lived until the early part of the next year, only to die one after another.

Evidently I had given them too little care and attention, being prevented by a somewhat lengthened absence from Freiburg, as well as by other labors.

I reached the conviction at that time that without the greatest carefulness and attention in the rearing no result can be obtained. This conviction further experience only confirmed. One must just concentrate all his interest upon this one aim, and must not begrudge having to devote considerable time every day for months to this work. That I could not carry this on myself, without giving up other work for it, seemed clear to me, and so I hailed it with joy when the opportunity offered of seeing the experiments made by another person.

Miss von Chauvin, a lady well known to several correspondents in this department by her beautiful observations on the Phryganidæ (alas, not yet published), proposed the following year to take a number of the larvæ just out of the egg, rear them, and make the attempt to bring them, in a certain measure, by force into the Amblystoma condition. It will be perceived by the following records of the lady herself how completely this attempt succeeded, and no less will it be seen that this success was possible only with such carefulness in the treatment and delicacy in the observation as were here employed.

EXPERIMENTS.

"I began the experiments June 12, 1874, with five larvæ about eight days old, all that remained alive of the twelve delivered to me. On account of the extraordinary tenderness of these larvæ, the quality and temperature of the water, the kind and quantity of the food supplied, especially in the earliest period, exert a great influence upon them, so that one can hardly be cautious enough in their management.

"The little creatures were kept in a glass globe of about 30 centimetres in diameter; the temperature of the water was regulated, and as nourishment Daphnida were furnished at first, afterward larger aquatic animals in greater quantity. In this way the five larvæ throve exceedingly well. By the end of June the strongest larvæ showed the beginning of the fore legs, and the 9th of July the hind legs made their appearance. At the end of November I noticed that one Axolotl—for brevity I distinguish it with I., and shall note the others with the successive Roman numerals—kept constantly on the surface of the water, which brought me to the supposition that the right time had come to prepare for the change to a land salamander.

"For this purpose, on December 1, 1874, I. was put into a considerably larger glass vessel with a flat bottom, which was so placed and filled with water that only in one spot could he dive quite under water, while everywhere else in his repeated creepings about the bottom of the vessel he came more or less in contact with the air. On the following days the

water was gradually diminished, and during this time the first changes in the animal appeared: *The gills began to shrivel.* At the same time the creature showed a striving to reach the shallow places. The 4th of December it betook itself wholly to the land and crept away into the damp moss which I had placed on a bed of sand in the highest part of the bottom. This was followed by the first molt. Within the four days from December 1 to 4 a striking change took place in the exterior of I.; the gill-tufts shriveled almost entirely together, the crest on the back vanished completely, and the hitherto broad tail assumed a rounded form similar to a land salamander's tail. The grayish-brown color of the body gradually changed to blackish; here and there white spots came out, faintly marked at first, and growing more distinct.

"When, on the 4th of December, the Axolotl crept out of the water, the clefts of the gills were still open, but they gradually closed, and in about eight days they were no longer to be seen and were grown over with a skin.

"Of the other larvæ, at the end of November (that, is at the same time when I. came to the surface of the water), three more were just as strongly developed as I.—an indication that for them also the right time had come for the hastening of the process. They were therefore subjected to the same treatment. II. changed in fact at the same time as I., and, precisely like it, had perfect gill-tufts when it was placed in the shoal water, and *after four days* had almost completely divested itself of these. He went upon the land; and then followed, in the *course of about ten days, the growing over of the gill-clefts and the complete assumption of the salamander's form.* During this last time the animal took food, but only when he was urged.

"With III. and IV. the change went on more slowly. They did not so frequently seek for the drier places, and generally did not expose themselves so long to the air, so that the greater part of January passed before they took wholly to the land. Yet the drying of the gill-tufts required no longer time than I. and II. The first molt also followed as soon as they crept upon the land.

"V. showed much more remarkable deviations in the transformation than III. and IV. As this individual from the beginning appeared much more feeble than the others, and also staid behind remarkably in its growth, this was by no means surprising. It required fourteen days instead of four to carry the change so far that it could leave the water. It was of quite peculiar interest to watch the condition of this individual during this time. As may be inferred from its delicate nature, it was more sensitive than the others to all outward influences. If it was exposed to the air too long it took on a lighter color. Besides it gave off a peculiar odor, similar to what salamanders diffuse when they are alarmed or endangered. As soon as these appearances were noticed, it was immediately put into deep water, where it dived under at once and gradually recovered again. Then the gills always unfolded again. The

same experiment was made repeatedly and was every time attended by the same result; from which it may well be concluded that through the exercise of too energetic constraint with a view to hasten the process of transformation a stoppage may be brought about, and death, indeed, by continued constraint.

"Of Axolotl V. it remains to be stated that he crept out of the water, not like all the others at the *first* molt, but at the time of the *fourth*.

"All these are to-day alive, healthily and strongly developed, so that, as regards their nourishment, nothing would stand in the way of their propagation. The largest of the first four has a length of 15 centimetres. Axolotl V. measures 12 centimetres.

"From what I have said must be established the correctness of the view suggested in the beginning: most Axolotl larvæ, if not all, complete their metamorphose, if, in the first place, they come out of the egg healthy and are properly fed, and, in the second place, meet with arrangements which force them to change from breathing under water to breathing above the water. It will be understood that this compulsion may only be exerted quite gradually, and in a way which does not draw too much upon the animal's vital force.

"Freiburg, Breisgau, July, 1875.

"MARIE v. CHAUVIN."

I remark upon the above records, that in all five cases the change was a complete one, not to be confounded with that which all the Axolotls confined in small glass vessels undergo more or less; namely, there are frequently variations which seem to advance toward the Amblystoma form without reaching it. In the five full-grown Axolotls which I possess at this very time, and of which two at least are four years old, the gills are all very much shriveled up, but tail and crest are unchanged. But the crest may also disappear and the tail grow smaller without changing to the Amblystoma, as shall be shown further on. As regards the time used for the transformation, in Axolotls I. to V. it took 12 to 14 days. Four days of that bring us to the first change, during which the animal still remains in the water; the rest of the time is given to the completion of the change. Duméril gives the time of the transformation at 16 days.

From the experiments communicated the following seems to me especially noteworthy: *The five Axolotl larvæ*, which alone can come into the account, since the others died early, *all without exception completed the change and became Amblystomas.* Only one of them, No. I., showed by constant swimming on the surface, which was noticed at the end of the sixth month, a distinct inclination to the change, a preference for breathing with the lungs. Of this individual, therefore, it may well be assumed, that also without artificial aid it would have come to the land and have undergone the transformation, just as was the case in some thirty specimens which Duméril observed.

For Nos. II., III., and IV., on the other hand, such a supposition has but little probability. All three larvæ sought to keep themselves in deeper water, avoided as long as possible the shallow places which compelled them to mere lung-breathing, and only completed the change more than a month later.

With No. V., moreover, it can scarcely appear doubtful that it would not have made the change without the forcible habituation to abode in the air.

From these results may well be drawn the conclusion, most Axolotl larvæ change to the Amblystoma form if at the age of six to nine months they are brought into water so shallow that they must chiefly breathe with the lungs. The experiments in question are small in number, to be sure, but such a conclusion cannot be called hasty, when it is considered that Duméril, among many hundreds (the number is not given precisely) of Axolotls, obtained only some thirty Amblystomas; that likewise, among several hundred Axolotls, von Kölliker bred only a single Amblystoma.

It only remains doubtful whether every larva can be compelled to make the change, and this question can only be determined by new experiments. It had been my intention to defer the publication of those above given until they were repeated in greater fullness by Miss von Chauvin. But as my Axolotls have given me no young this year (1875), I had to give that up for the time, and could do this the more willingly, since it is rather irrelevant to the theoretical interest of the facts whether *all* or only *almost all* of the Axolotls may be forced to make the transformation. On the other hand, I will not forbear to mention, that the curator of the zoological museum here, Herr Gehrig, reared a considerable number of larvæ from the same brood, with which Miss von Chauvin experimented, and that of these larvæ six passed through the winter *without undergoing the transformation.* They were always kept in deep water, and therefore constituted the counter-experiment to those communicated above, showing that this whole brood by no means possessed a predisposition to undergo the transformation.

If, now, these new facts are to be made use of to clear up our conception of the nature of this unusual process of transformation, we must, before all else, bring to our aid the data already known.

In the first place, it is to be laid down that *Siredon Mexicanus, in its home, so far as we know, never undergoes the transformation. From that locality it is known only in the Siredon form.* The testimony which I find on this point comes from DE SAUSSURE,* who himself observed the Axolotl in the Mexican waters. This naturalist has never seen even a single Amblystoma in the vicinity of the lakes, and "yet the larvæ of the Axolotl are so common there, that they are brought into market by thousands." De Saussure believes that the Axolotl does not make the change in Mexico.

* Verhandl. d. Schweiz. Naturforsch. Gesellschaft. Einsiedeln, 1868.

Cope* asserts the same thing quite decidedly; and individuals bred by him in America from the *Siredon Mexicanus*, also in captivity, "showed no inclination to the transformation." On the other hand, Tegetmeier† saw the change begun in one of five individuals which traced their descent to the Lake of Mexico and so the second fact is established, *that also the genuine and real Axolotl under certain circumstances changes in confinement to an Amblystoma.*

This remark would be superfluous, if it were, as was long believed, true that the Axolotl of the Paris Garden of Plants, whose metamorphosis was first observed and excited so much attention at the time, actually belonged to the species *Siredon Mexicanus*, the only *Siredon* which in its home bears the name Axolotl.

In his first communication, Duméril himself was of this opinion; he called the creature "*Siredon Mexicanus*" syn. *Humboldii*;‡ but later, in his detailed work§ on the change of the Axolotl contained in the Garden of Plants, he recalled this view, and, after a critical examination of the five described *Siredons*, came to the conclusion that the Axolotls in the possession of the Paris Museum were probably *Siredon lichenoides* Baird.

So all the transformations of Axolotls observed in Europe were to be referred to this species; for—at least so far as is known—they are all descendants of the Paris colony. Thence also, indirectly, came the subjects of my experiments.

To be sure, now it does not agree with this, that the Amblystoma form, which Duméril obtained from his Axolotls, corresponded with *Amblystoma tigrinum* Cope, while we learn by Marsh‖ that *Siredon lichenoides* Baird changes to *Amblystoma mavortium* Baird when it undergoes the complete metamorphosis. Marsh found the *Siredon lichenoides* in Alpine lakes (7,000 feet above the sea), in the southwestern portion of the United States (Wyoming Territory), and by breeding in aquariums obtained from it the *Amblystoma mavortium* Baird. Nevertheless, he holds it doubtful whether the animal ever goes through the change in its home; to be sure, without any sure foundation and on purely theoretical grounds, namely, because in his judgment "the colder temperature there is less favorable to it."¶

If I doubt the correctness of this last opinion, it is only because the *Amblystoma mavortium* in a state of nature has been found in many parts of the United States, namely, in California, New Mexico, Texas,

* Dana and Silliman, Amer. Journ., 3d series, i, p. 89. Annals Nat. Hist., vii, p. 246.

† Proceed. Zool. Soc. 1870, p. 160.

‡ Compt. Rend., tome 60, p. 765 (1865).

§ Nouvelles Archives du Muséum d'Hist. Nat. Paris, 1866. Tome ii, p. 268.

‖ Proceed. Boston Soc., vol. xii, p. 97; Silliman, Amer. Journ., vol. xlvi, p. 364; a reference to this in Troschel's Jahresbericht for 1868, p. 37.

¶ Proceed. Boston Soc., vol. xii, p. 97; Silliman, Amer. Journ., xlvi, 364. I could not examine these works myself, and quote from the reference in Troschel's Jahresbericht, 1868, p. 37.

Nebraska, and Minnesota. Nevertheless, it is by no means incredible that just in the Alpine lakes, from which Marsh obtained it, the species occupies a different position in regard to the transformation from what it does in other habitats. This will be seen from the observations on the Triton adduced below. So, until further observations are made, I believe we must suppose that the Paris Axolotls are not *Siredon lichenoides*, but probably a new and very closely related species.

Meanwhile, there is not much depending upon this in the review of the transformation, if it is only established that this Axolotl in its home does not undergo the metamorphosis, or only does it as exceptionally as in Europe. Unfortunately, there is in Duméril's communications no precise statement of the locality where this "Mexican" animal was found; probably the locality was unknown to himself, and so I can only assume on Cope's authority that no *Amblystoma* has ever been brought from south of the provinces of Tamaulipas and Chihuahua; that is, from south of the tropic.*

Of that, however, there is no certainty. Much more important is the fact adduced above, that the genuine Axolotl of the lakes around the city of Mexico never makes the change to an Amblystoma, but that this species also in isolated cases undergoes the transformation in confinement. Now, from this and from the fact that the Paris Axolotls in confinement are only transformed to the extent of a very small percentage, it may be concluded *that also in its home it is either not transformed at all, or only as an exception.*

But still another series of facts comes very essentially into the account in reviewing this history of transformation: I mean *the existence of a considerable number of species of Amblystoma in nature.* In the "Revision der Salamandriden-Gattungen" (Review of the genera of Salamanders) which Strauch † gave a few years ago, there are represented, according to the examples of Cope,§ *twenty* species of the *Amblystoma* Tschudi living in North America. Now, although a few of these species are based only upon *one* specimen, and, therefore, as Strauss correctly says, "must be suppressed in time," yet there is left a whole range of species which certainly live and propagate as Amblystoma, and which have their locality from the latitude of New York to that of New Mexico. *Hence there are certainly species of Siredon which, under their natural conditions of life, regularly take the Amblystoma form and propagate in it; while on the other hand there are at least two species which, under their present natural conditions of life, only propagate as Siredon.* It is only another form of expression for this fact when one says the Mexican Axolotl, and the Paris Siredon as well, be this latter named *lichenoides* or something else, stands *upon a lower phyletic stage of development* than the other species of Amblystoma which propagate in the salamander

* Dana and Silliman, Amer. Journ., 3d ser. i, p. 89; Annals of Nat. Hist. vii, p. 246.
† Proceedings Acad. Philad., xix, 1867, pp. 166–209.
§ Mem. Acad. Petersb., tome xvi.

form. No one can object to this statement; while the other proposition, either expressed or tacitly held by all authors, includes a theory which I regard as incorrect. That proposition is: The Mexican Axolotl has *remained* upon a lower phyletic stage of development.

All zoologists who have expressed themselves on the transformation of the Mexican Axolotl, and who are not, like its first observer, still attached to Cuvier's views on the immutability of species, took up the matter as if here was a species which through some sort of special circumstances had *remained behind* on a lower stage of development, and was now stimulated by some sort of influences to its *advance* to a higher stage.

For a long time also I did not believe that the thing could be otherwise understood, little as I was able to bring all the phenomena into harmony with this view. Thus in 1872 I used the following expressions:* "Why should not a sudden change in all the relations of life (the removal from Mexico to Paris) have had a *direct* influence upon the organism of the Axolotl, so that he *suddenly* attained a higher stage of development, which many of his kindred species have long since attained, which evidently lies in the nature of his organization, and which perchance he also would have reached in his native haunts, though at a later period? Or would it be too much to suppose that by the sudden transportation from 8,000 feet above the sea-level (the Mexican highland) to the altitude of Paris, the organs of respiration had received a shock which just brought them to the change already close at hand? So in all probability we have to do with a direct effect from altered conditions of life."

That the purport of the last sentence must also be held true to-day follows as a matter of course from the experiments communicated above, which surely prove that by the application of definite external influences we have to a certain extent it in our power to call forth the transformation. Just in that fact lies the new light which these experiments have brought.

But must we also understand the phenomenon in the manner above indicated—that is to say, as *a phyletic onward development of the species, appearing suddenly and in a measure resulting from a shock?* I believe not. What first perplexed me in regard to this view was the sight of my living Amblystomas reared from the larvæ of the Axolotl. These creatures by no means show a variation from the Axolotl in single traits merely, but they are distinguished from it in their entire habit; they differ somewhat in all parts; although slightly in many, in others quite decidedly; in short *they have become entirely different animals.* Corresponding to this they also live quite differently; no longer go into the water, but prefer in the daytime to keep hidden in the damp moss of their prison, and at night come forth to seek their food on the dry land.

*"Ueber den Einfluss der Isolirung auf die Artbildung" (On the Influence of Isolation upon the Formation of Species), Leipsic, 1872, p. 33.

To be sure I could have perceived the great difference between the two stages of development from the anatomical data long familiar to me which Duméril had given on the structure of his Amblystomas; but the reading over of many statements in detail gives no living picture. At any rate the sight of the living animal first brought me to the consciousness how comprehensive is the change we have to do with here; that by no means does it merely concern those parts which are directly affected by the alteration in the mode of life, but that most, if not all, parts of the animal undergo a transformation, which can be very well explained in part as the morphological adaptation to new conditions of life, in part as consequences of these adaptations (correlative changes), *but cannot by any possibility be explained in a word as the suddenly appearing effect of these changed conditions of life.* Such at least is my view, according to which a sudden development of the species, such as must have taken place here, is quite inconceivable. I willingly acknowledge that a few years ago the question whether such sudden development occurs was still an open one for me, but since then my investigations have kept urging me to the conviction that it does not occur at all, as I shall show in another place. Here I have to confine myself to the examination of this individual case; a case which appears to me—as was above intimated—quite peculiarly suited to shed light decisively upon the great alternative, about which at the present moment the war of opinions is centered, in regard to the doctrine of descent.

I may well assume that hitherto it has been with most students in regard to the metamorphosis of the Axolotl very much as with myself; it did not come to their consciousness *how far the transformation goes;* and so it may need to be made plain that the theoretical importance of the case and its value as a basis of inference was not properly emphasized by either side. But it is evidently a case of quite unusual significance for the principles involved. I believe it may be easily shown that the hitherto pretty generally admitted explanation of the history of the Paris Axolotl's transformation includes at the same time the recognition of a very far-reaching principle, namely: if this explanation were the correct one, then in my judgment would be at the same time demonstrated as correct the opinion of those who, like KÖLLIKER, ASKENASY, NÄGELI, and among the philosophers HARTMANN and HUBER, would refer the transmutation of the species in the first instance to a motive power dwelling within the organisms, to an active, *i. e.* spontaneous, "law of development," a "principle of perfection," or, as I should prefer to name it, a *phyletic vital energy*, in contrast to the exactly corresponding vital energy of the so-called "philosopher domain" in the nature of ontogenesis.

If, namely, the Axolotls that have become Amblystomas are to be taken as individuals which, stimulated by external influences, have hastened on in advance of the remaining individuals in their phyletic development, then this advance can only be placed to the account of a phy-

letic vital energy; for the transformation is a sudden one; it leaves no time for gradual adaptation in the course of generations. *Indirect* influence of the external relations of life, *i. e.* natural selection, is accordingly excluded from the first; but *direct* influence of the altered circumstances of life does not suffice by a great way to explain the total transformation of the whole structure, as I have already intimated and will now show more minutely.

The distinctions between the Paris Axolotl and its resulting Amblystoma are, according to DUMÉRIL, KÖLLIKER, and my own observations, the following:

1. The gills disappear, the clefts of the gills close up, and only the foremost of the arches of the gill remains in existence; the other arches vanish. At the same time the *Os hyoideum* is changed (DUMÉRIL).

2. The crest on the back disappears entirely (DUMÉRIL).

3. The rudder-like tail changes to a tail like a salamander's (DUMÉRIL), which nevertheless is not quite circular in section as in the salamander, but is somewhat compressed laterally (WEISMANN).

4. The skin gets yellowish-white patches, irregularly distributed on the sides and the back (DUMÉRIL), while at the same time its former ground color of grayish-black changes to a shining greenish-black (WEISMANN), and, besides, the shiny secretion from the skin is lost and the glands of the skin become indistinct (KÖLLIKER).

5. The eyes become prominent and the pupils small (KÖLLIKER), and eyelids are formed which can close the eye completely, while in the Axolotl only a narrow circular fold surrounds the eye, and it cannot be closed (WEISMANN).

6. The toes diminish in size and lose their skin-like appendages (KÖLLIKER), or, more precisely, the half web-membranes which unite the inner ends of the toes on all the feet (WEISMANN).

7. The palatal teeth in this, as in all Amblystomas, stand in a diagonal row, while in the Axolotl, like the Triton larvæ, they stand at the side of the palatal vault forming an arched band, with several rows of teeth.* (DUMÉRIL. See his figure. Zeitschrift f. wissensch. Zool., xxv Bd., Sup., p. 279.)

8. In the Axolotl the under jaw has, besides the teeth on the upper edge of the bone, some very small teeth disposed in several rows; these latter disappear after the metamorphosis (DUMÉRIL). I add that the permanent teeth belong to the *os dentale*, the temporary ones to the *os operculare*.†

* DUMÉRIL has the teeth of the vomer separated from those of the *os palatinum* by a gap. Probably this was an artificial one, as GAGENBAUR (FRIEDRICH & GAGENBAUR: "Der Schädel des Axolotl"—The Skull of the Axolotl—Würzburg, 1849) figures the rows of teeth without interruption, passing over from one bone to the other. The same was true in three Axolotls which I examined in regard to this point; moreover, this little difference is quite unimportant in the question here treated.

† See O. HERTWIG, "Ueber das Zahnsystem der Amphibien und seine Bedeutung für die Genesis des Skelets der Mundhöhle." (On the Dental System of the Amphibia, and its Significance for the Genesis of the Skeleton of the Mouth.) Arch. f. Mikroskop. Anat., Bd. xi, Supplementheft, 1874.

9. The posterior face of each vertebra is slightly hollowed out before as after the transformation, but the anterior face is less concave in the *Amblystoma* than in the *Siredon* (DUMÉRIL).

The details cited from DUMÉRIL under 7 and 9 I have not so far been able to confirm by personal examination, as I was not willing to kill any of my *living* Amblystomas, only for the purpose of verifying the details of a naturalist in whom perfect confidence may surely be reposed. In like manner, I have not yet seen the change in the arches of the gills. All the other data given by KÖLLIKER or DUMÉRIL I can corroborate completely.

The differences in structure which exist between Axolotl and Amblystoma are considerably greater and more important than those between neighboring genera, yes, greater than are found between the *families* of the *Urodela*. The genus *Siredon* without any doubt belongs *to a different suborder* from the genus *Amblystoma*, into which it is occasionally transformed. STRAUCH, who has made the latest arrangement of this group, separates the suborder of the *Salamandrida* from that of the *Ichthyodea* by the possession of eyelids and by the position of the palatal teeth in a simple row on the posterior edge of the palatal bone; while in the *Ichthyodea* the lids are wanting and the palatal teeth either "stand on the front edge of the palatal bone or cover the whole surface of the palate as brush-like clusters." How would it be possible now to regard anatomical characters standing so far asunder as transformations which had been suddenly called forth by a single operation of varying conditions of life?

Hand in hand with the falling out of the old palatal teeth and the appearance of new goes a change in the anatomical structure of the vertebral column, and, as we may conclude from KÖLLIKER'S entirely accurate observation on the stoppage of the slimy secretion from the skin, in the histological structure of the skin itself.

Who would undertake to explain all these deep-lying changes as the direct and sudden effect of any external influences whatever *operating but once?* And even if any one had an inclination to explain them *as results of the loss of the gills*, and therefore as *correlative changes*, what would such a *correlation* be but the newly-christened vital energy above spoken of? For if from *one* variation caused by direct influence of *external* agencies the whole body can through correlation transform itself in a couple of days just so in all its parts *as it appears best adapted for the new conditions* of life in which it is henceforth to be, then the word correlation is only a term, by which nothing is explained, but the search for a better explanation is hindered. Then it is preferable that we simply acknowledge our belief in a phyletic vital energy.

Moreover it certainly is not allowable even to wish to seek an explanation of that sort (by correlation), *for we know some Urodela in the adult state have no gills, and yet possess all other marks of the Ichthyodea:* lack

of the eyelids, characteristic type of the palatal teeth, and of the arrangement of the lingual bones. Such are the genera *Amphiuma* L., *Menopoma* Harl., and *Cryptobranchus* v. d. Hoev. The first two genera, as is well known, still have the clefts of the gills. *Cryptobranchus*, on the contrary, has lost these clefts, which are grown over with skin as in the *Amblystoma*, and yet, by the unanimous testimony of all systematic zoologists, it is a genuine fish-lizard in habit, arrangement of the lingual bone, palatal teeth,* &c. It must be added *that even the Axolotl itself may lose the gills without, on that account, changing to an Amblystoma.* I have mentioned elsewhere that in Axolotls which are kept in water that is shallow and still, the gills frequently grow small; but it also happens that they shrivel up entirely. I have an Axolotl preserved in spirits, in which the gills are shriveled to little irregular bunches; at the same time the crest on the back is so completely wanting that a longitudinal furrow has appeared in its place, and on the tail the border of skin has entirely vanished from the lower margin, and about half from the upper. Nevertheless, the animal is widely separated in structure from the Amblystoma: it has the arches of the gills, the palatal teeth, the skin, &c., of the Axolotl.

This demonstrates, therefore, that the loss of the gills by no means must always bring after it all the other variations which we see take place in the metamorphosis of the Axolotl; that these, therefore, are by no means the necessarily and immediately appearing result of that loss. Whether they must necessarily appear after long successions of generations, whether also the descendants of *Cryptobranchus* will some time in the future take the structure of the *Salamandrida*, that is another question which I should not like to answer just in the negative, but which does not come into the account here, as we are considering only a possible *sudden* result from the loss of the gills.

The question, therefore, seems to stand thus: *Either our apprehension up to this time of the transformation history of the Axolotl as a further development of the species is incorrect, or the existence of a phyletic vital energy is demonstrated by the case of the Axolotl beyond the possibility of a refutation.*

Now the question comes up, whether the facts of this transformation history do not also admit of another explanation. I believe that this is at any rate possible and that another interpretation may be shown as the correct one with a good degree of probability.

I esteem those Amblystomas which in individual cases have developed in confinement from Siredon Mexicanus (syn. piscifórmis), as well as from the Paris Axolotl, not as forms of advancement, but forms of retrogression. I believe that the Axolotls which to-day live in the lakes of Mexico were already Amblystomas a geological (or better a zoological) epoch earlier, but

* See Strauch, Zeitschrift. f. Wissensch. Zool., xxv Bd., Suppl., p. 10.

that through alterations in their conditions of life they have sunk back to their earlier stage of the Perennibranchiates.

Without doubt I was first led to this intepretation by the results I had reached in my studies on the season-dimorphism of butterflies.* There also we have the question of two different forms under which one and the same species appears, and of which it may be proved as probable that one is phyletically the older, the other the younger. The younger summer form has in my view proceeded through the gradual warming of the climate from the winter form that in an earlier zoological epoch was the only one; but this latter, the primary form, has not on that account ceased to exist, but to-day still alternates every year with the secondary, the summer form.

Now it is easy with the season-dimorphous butterflies to make the summer brood assume the winter form, and that by exposing their pupæ rather a long time to a lower temperature; and it may be made in the highest degree probable that this suddenly appearing variation or transformation, often very far reaching, is sudden in appearance only, and is but apparently the result of cold acting upon this generation. Much rather in truth the variation depends upon a reversion to the primary form of the species, and therefore the cold that appears but once is only the *impulse to the reversion*, but not the *true cause of the transformation*. This cause must be sought in the long-continued operation of the cold, to which thousands of generations of the ancestors of our living butterflies were subjected, and whose final result was just the winter form.

If we now assume for a moment that my interpretation of the Axolotl's transformation-history as just given is correct, we have relations here which are in many respects analogous to those of the season-dimorphism. To be sure the two forms in this case no longer alternate regularly with each other, but the primary form may occasionally appear in place of the secondary, and this result from the shock of external circumstances. As *there* we succeed in stimulating the summer brood by the action of cold to lay aside the summer form and adopt the winter dress, so *here* we are able to lead the Axolotls into the Amblystoma state by compelling them at a certain age to breathe air.

Further, as in the season-dimorphism, it may be shown that this transformation called forth by artificial means is *only in appearance* a sudden new formation, but in truth a reversion to the much older winter form, so here we also had to do, not with an *actual* new formation of the species, but only with an *apparent* one, a reversion to the phyletically older form of the species. To be sure that sounds very paradoxical if here is a form that must have come by reversion, and yet it must undoubtedly be accounted as the *more highly* developed. But I believe

* Studien zur Descendenztheorie, I. Ueber den Saison-Dimorphism der Schmetterlinge (Studies on the Doctrine of Descent, I. On the Season-Dimorphism of Butterflies), Leipsic, 1875.

that on more careful consideration much of the paradox which seems to lie in this view will disappear.

Before all else, it is to be considered that the phyletic development of the species need by no means have always gone directly forward. We have examples enough of development backward, although in rather a different sense, as in parasites and such forms, which have sunk from free locomotion to the sedentary mode of life. I do not ignore the difference which exists between this sort of development backward by the pining away of certain organs or systems of organs, and proper reversion. The latter is *the return to an animal* form *already once existent*, but in the former case, in spite of all simplification of the organization, *something wholly new* is always formed. But I am able to see nothing absurd as to principle in the supposition that a proper reversion, also, be it of a whole species or of the individuals of a species within a certain habitat, is thought of as *possible*, and I do not for the present demand a further concession. Why, for example, should it be so entirely incredible that the Axolotl, in a time long past, was adapted to living on the land, that it *gradually*, through direct and indirect operation of altered conditions of life, had acquired the salamander form, but that later, by a new change of the circumstances of life unfavorable to its present organization, it has again fallen back into the old form or one lying near it? At any rate, such a supposition contains nothing which would stand in contradiction with well-known facts, but can be sustained in several ways; and finally, it recommends itself by furnishing, at least in my opinion, the only possible explanation of the facts before us.

The above-mentioned existence of a whole group of species of *Amblystoma* shows at once that species of *Siredon* can rise to the salamander form, and can regularly propagate in that form; and further, that this phyletic advance has already actually taken place in very many species. But that a sinking back from this higher stage of development to the lower can also take place, several observations on our water salamanders show.

It is well known that Tritons under some circumstances become, as it is usually expressed, "sexually mature in the larval state."

In the year 1861 De Filippi* found in a swamp by Lake Maggiore fifty Tritons, of which only two showed the structure of the full grown water salamander; but all the others still had their gills, yet corresponded to mature animals in bodily size and in the development of the sexual organs, and that in both sexes.

Filippi determined the fact that these "sexually mature larvæ" did not merely resemble larvæ externally by the possession of gills, but that they also presented all the other anatomical marks of the larvæ; that is, the characteristic clusters of palatal teeth standing on both sides, instead of the later simple row, and a vertebral column, which still has the *Chorda dorsalis* running through its whole length.

* Sulla larva del Triton alpestris, Archivio per la Zoologia, 1861.

According to my view this would be *a case of reversion of the Triton to the phyletic stage lying next behind it, that is, the Perennibranchiate stage;* and in this case most zoologists who stand at all upon the footing of the doctrine of descent will agree with my view. I at least would count it a profitless playing with words if any one should speak here of larval reproduction and believe he had thereby explained anything. In any event the animal becomes sexually mature in the condition in which it first appears as a larva. But we first get an insight into the nature of this phenomenon by the reflection that this so called "sexually mature larva" has precisely the structure which the preceding phyletic stage of the species must have possessd; that therefore we have a reversion of the individual to the older phyletic stage of the species. I esteem it an error when DUMÉRIL puts this case of the Triton in parallel with the genuine larval reproduction of WAGNER'S *Cecidomyia* larvæ. There it is certainly not reversion to an older phyletic stage which makes the larvæ capable of reproduction; for these larvæ present no older phyletic stage of the species, but *must have arisen at the same time with the species in its present form.* The vast difference in the structure of the larva and the fly is not explained by assuming that the latter has arisen from the former as from a finished given quantity, but by this, that both at the same time have adapted themselves to conditions of life further from each other.* Regarded phyletically, these larvæ are not at all a necessary point of transit for the origin of the fly. They could also be built quite otherwise, without the form of the fly needing to be likewise changed; for the stages of insect transformation vary independently of each other, corresponding to the conditions of life to which they are subjected, and exert no influence upon each other, or only a very slight one, in the determination of form, as I shall attempt to demonstrate in another place. At any rate, "the ability of these larvæ (the *Cecidomyia*) to multiply asexually has first been acquired as a secondary matter, as already follows from the fact that there are numerous species of the same genus of flies which do not feed their young." "In the form which they possess to-day they can never have played the part of the final stage of ontogenesis, and therefore also cannot have possessed at a former time the power of sexual reproduction.† In short, we have to do here with genuine larval reproduction, but in the Tritons with reversion to an older phyletic stage.

Nor can I agree with my friend HAECKEL, when he designates the reversion of the Tritons as "adaptation to continued life in the water."‡

One would only be able to speak of "adaptation" in this case by taking the word in a sense quite different from that with which DARWIN

* Compare, also, LUBBOCK, On the Origin and Metamorphoses of Insects. London, 1874.

† See my paper "Ueber den Saison-Dimorphismus der Schmetterlinge," Leipsic, 1875, p. 60.

‡ See HAECKEL'S Anthropogenie, p. 449.

and WALLACE have introduced it into science. Those naturalists distinguished by the word a gradual remodeling of the body, taking place in the course of generations, corresponding to the new demands of new conditions of life; in other words, the operation of natural selection, but not a result from causes of variation suddenly and directly acting once and in one generation.

Just because the word "adaptation" may, according to customary use of language, be used in many different senses, it would be desirable to take it only in *one* acceptation and to have that fixed exactly; before all, not to speak of adaptation when there is no *morphological* change, but only a sort of exchange of functions in DOHRN'S sense.* Thus, for example, when FOREL† shows that fresh-water air-breathing snails, whose organization is calculated for the direct breathing of the air, could nevertheless pass to the greatest depths of the Alpine lakes, while they used their lungs as gills. That with this not the slightest change has taken place in the lungs, is shown by the observations of v. Siebold.‡

He saw the Pulmonates of shallow water use their lungs alternately for direct air-breathing and for water breathing, according as the atmospheric contents of the water was less or greater. If with v. Siebold one should apply the word "adaptation" simply to such cases, it would lose the special sense which was originally attached to it; as a technical term the word would have to be given up.

At any rate, there is as little a case of genuine adaptation in the Triton "larvæ" that were capable of reproduction as in the Axolotl exceptionally changing to the Amblystoma. In both cases, also, the transformation in consideration is not at all indispensable *for the life of the individual.* Mature Tritons (without gills) live, as I have witnessed, many months, probably for years, in deep water, although they are fitted for simple air-breathing; and Axolotls, as I have already stated above, can live quite well for years in shallow and quiet water. If their gills shrivel, yes, vanish entirely, this also yet is no adaptation in the Darwinian sense, but a direct result of external influences, principally indeed of diminished use.

A case quite analogous to FILIPPI'S was observed in 1869 by Jullien. Four female larvæ of *Lissotriton punctatus* Bell. (synonym for *Triton taeniatus* Schnd.) were fished out of a swamp and showed themselves sexually mature. In their ovaries they had matured eggs, ready for laying, and two of them also actually laid the eggs. Four male larvæ, which were taken in the same swamp, showed themselves likewise developed in regard to bodily size, though they had no spermatozoa in the testicles, but only sperm-producing cells.§

* "Der Ursprung der Wirbelthiere und das Princip des Functionswechsels" (The Origin of the Vertebrates and the Principle of the Exchange of Functions). Leipsic, 1875.

† Faune profonde du lac Léman; Verhandl. d. Schweiz. Naturforsch. Gesellschaft (Deep Fauna of Lake Geneva). Schaffhausen, 1873.

‡ Zeitschrift f. Wissenschaftl. Zool. (Journal of Scientific Zoology), bd. xxiii, 1873.

§ Compt. Rend., t. lxviii, p. 938, 939 (Proceedings of the French Academy of Sciences).

A third case of the same kind I find cited* by SEYDIG, in his essay, "Ueber die Molche der Würtembergischen Fauna" (On the Salamanders in the Fauna of Würtemberg), so rich in interesting detail. SCHREIBERS, the former director of the Vienna Cabinet of Natural History, likewise found "larvæ" of Triton with gills well developed, but of the size of "adult males," and, as anatomical examination showed, with well developed sexual organs, as well as ovaries filled with eggs.

So, therefore, it is established that species which long ago attained the stage of Salamandrida in the phyletic development may occasionally sink back to the stage of Perennibranchiates. Evidently, this fact makes my view of the Axolotl as a form of reversion appear much less paradoxical. Indeed, the cases of reversion in the Triton are directly analogous to the transaction I suppose for the Axolotl.

We only need suppose Amblystomas in the place of the Tritons, and consider the swamp in which DE FILIPPI found his "sexually mature Triton larvæ" expanded to the Lake of Mexico, regarding, also, the unknown, and perhaps in this case temporary, causes of the reversion as permanent, and we have everything which is necessary to the restoration of the Axolotl as we know it to-day, *we obtain a Perennibranchiate population of the lake.*

It is not even yet determined whether, in that swamp of DE FILIPPI the Perennibranchiate form of the Triton does not actually prevail *permanently*, for it has not, to my knowledge, been examined since in regard to this subject.

But if we assume for a moment that it actually were so, that a colony of Perennibranchiate Tritons lived there, carrying on reproduction sexually, should we wonder if occasionally, also, a genuine Triton came from our brood, if we could succeed in stimulating most individuals of this brood by removal into shallow water to the metamorphosis into Tritons? But just so it is according to my view with the Mexican Axolotl.

But I need not limit myself to support my hypothesis, but must also directly assail the tenability of the one hitherto held, for it stands in opposition to facts.

If we really had in the Axolotl a suddenly occurring phyletic further development, then one fact would remain wholly incomprehensible, namely, *the sterility of the Amblystomas.*

Of about thirty Amblystomas which Duméril had obtained up to the year 1870, full sexual maturity had not appeared in a single one; neither copulation nor the simple laying of eggs had taken place, and the individuals that were examined anatomically showed the eggs immature and the spermatozoa present indeed, but without the undulating membrane belonging to all the Salamandrida. They were not destitute of all power of motion, but as QUATREFAGES stated, only moving imperfectly.†

* Archiv f. Naturgeschichte (Archives for Natural History), 1867.

† Compt. Rend., t. lxx, 1870.

The five Amblystomas, on which I have reported here, have shown, up to the present time, no appearances of reproduction.

It is evidently an objection that will very poorly stand the test when SACC* attributes the sterility of the Amblystomas reared from Axolotls to "poor food." Why, then, do the Axolotls reproduce so easily when they are fed exactly the same? I can also state expressly that my Amblystomas are quite excellently fed. To be sure, these have hardly reached the age of one and a half years; but the Axolotls propagate the second year, and some of DUMÉRIL'S Amblystomas were five years old in 1870.

The fact of sterility stands in clear opposition to the view that these Amblystomas are the regular advanced guards of the genus Siredon as it moves forward in phyletic development. To be sure I will by no means maintain that my theory of reversion could actually explain the sterility, but at least it does not stand directly in contradiction with it. Mere forms of reversion may perish without reproducing themselves. A *new* form called forth by the working of an unknown phyletic vital energy cannot be a sterile one, because this directly destroys again the "purpose" which the vital energy is pursuing. The idea of the vital energy includes that of teleology.

Moreover, from our stand-point the sterility of the Amblystomas may be, if not completely understood, yet shown as a phenomenon that does not stand quite alone. In the case of the *Lissotriton punctatus*, as quoted above, the *female* "larvæ" were at any rate sexually mature and laid eggs, but at the same time the *males* had no perfected spermatozoa in the testicles.

Other cases of the kind are not known to me. At the time when I made my experiments with butterflies, as mentioned above, this point of view was still unseen, and so I neglected to examine the artificially produced forms of reversion in regard to their organs of generation. But general principles also lead to the conclusion that atavistic forms may easily remain sterile.

DARWIN* finds the most immediate causes of sterility, first, in the operation of widely varying circumstances of life; and, second, in the crossing of individuals with widely differing constitutions. Varying circumstances of life are at any rate what induce the transformation of the Axolotl, and from this point of view it could not be surprising if we find those individuals sterile, which have precisely shown themselves as especially affected by these altered conditions of life, since they have reverted to the salamander form. In this reasoning it is by no means asserted that *reversion always and without exception* is accompanied by sterility. Nor can it be objected to my interpretation of the Axolotl's transformation that through reversion a colony of Axolotls capable of reproduction never could have arisen. On the contrary, JULLIEN'S female Triton

*Bull. Soc. Neuchâtel, Bd. viii, p. 192, a reference to the place in Troschel's Jahresbericht (Annual Report), for 1869.

*Origin of Species, 5th edition, p. 325.

larvæ that laid eggs exactly prove that even in reversion the power of reproduction may remain complete. From the universal causes of sterility mentioned above, it may be inferred that through those causes fruitfulness may be lost in *different* degree; and, further, it may in a measure be understood why the fruitfulness is more completely lost in the reversion to the Amblystoma form than in the reversion of the Triton to the Perennibranchiate form.

If in these cases the reversion is called forth by altering the conditions of life, one may perhaps imagine that the extent of this alteration will also fix the degree of fertility which the atavistic form can preserve; but still more will the fertility be influenced by *the extent of the morphological skip* which is made in the reversion.

We know that the blending of widely varying constitutions (*e. g.*, in the crossing of different species) produces sterility. Something similar takes place also in the sudden reversion to a stage of development widely varying in its whole structure. Here also takes place to a certain extent the union of two very different constitutions in *one* individual, a sort of crossing.

From this point of view it may be, to some extent, understood why sterility may be a result of the reversion, but, on the other hand, we obtain no explanation why with the same breadth of morphological variation there occurs in one case complete sterility, in the other relative fruitfulness. The extent of the morphological contrast is exactly the same between Axolotl and Amblystoma as between Triton and its "sexually mature larvæ." The difference in the two cases of reversion lies entirely in the direction of the skip, which in the first case is made exactly in the contrary direction to that in the second.

Just in that I would seek the reason for the varying force with which the power of reproduction is affected; not in the direction of the leap *in and for itself*, but in the differences of the ontogenesis, which are conditioned upon the direction of the leap.

The *reversion* of the Triton to an *older phyletic stage* coincides with *remaining* upon a *younger ontogenetic* stage; or, in other words, *the older stage of phylogenesis, to which the reversion takes place, is still entirely included in the ontogenesis of every individual.* Every Triton is a Perennibranchiate for a considerable portion of its life; the individual that makes the reversion simply reverts to an older phyletic stage by remaining in the larva stage of its individual development.

Quite otherwise with the reversion of the Axolotl to the Amblystoma form, which had been once reached at some former time, but long since given up. *This is not included in the ontogenesis of the Axolotl, but has entirely fallen out.* For a long succession of generations—so we must suppose—the ontogenesis has always proceeded only to the Perennibranchiate form. If now single individuals are made to revert to the Amblystoma form, no greater leap in respect to morphology is made than in the reversion of the Triton to the Perennibranchiate form. At

the same time it involves a leap in an opposite direction, namely, a leap away over a long succession of generations, back to an animal form, which for a long time the species had not produced, which to a certain extent had become foreign to it.

We should therefore have here also the coincident effect upon the Axolotl's constitution of a widely different constitution, or—if one prefers—the blending of two widely varying constitutions.

Of course I am very far from wishing to give this explanation for an exact one. It is nothing more than an attempt to point out the force in which we are to seek for the cause of the varying extent to which the power of reproduction is affected. To investigate more deeply and to demonstrate specially in what manner this force comes into operation must be left to a later time. For the present it must suffice to have shown in this connection that in general an essential difference exists between the two kinds of reversion, as well as to have made it in some measure comprehensible that this difference may be the motive force in relation to the question of sterility. Perhaps the law involved here may some day be formulated thus: *Ataristic individuals lose the power of reproduction the more completely as the series of generations of their ancestors is longer whose ontogenesis no longer contains the phyletically older stage to which the reversion takes place.*

Consequently our hypothesis, which regards the transformation of the Axolotl as a reversion, offers us at once the possibility of learning to understand the sterility of the Amblystomas produced from Axolotls. So on the contrary the observed sterility of these Amblystomas is for those who think that a phyletic vital energy was here exerted—let it be named whatever it may—not only "a veritable scientific enigma," as DUMÉRIL expresses himself, but a complete parodox. Of such a designing, impelling principle it ought to be expected that it would bring forth new forms capable of life and not decayed to the point of dying out; and this so much the more since there is concerned a combination of structural peculiarities, which, when it has originated in another way (namely, from other species of *Siredon*), *has already long ago shown itself capable of life and reproduction.* We know species of Amblystoma which reproduce as such, and every one of which comes from a larva like the Axolotl. One cannot, therefore, explain the sterile Amblystomas which the Paris Axolotl produces as an unsuccessful effort of the vital energy—an explanation, which to be sure, would be in and for itself sufficiently presumptuous.

But now it may be asked, *What change in the conditions of life could it have been* which made the *Amblystoma in the Lake of Mexico** revert to the Siredon form? To be sure, I can only answer this question with conjectures, which can claim but a limited value so long as they cannot be sustained by a more exact knowledge of the circumstances there and the habits both of the Axolotl and the Amblystoma.

*As we do not know the origin of the Paris Axolotl, I must confine myself in the following to *Siredon Mexicanus* Shaw.

In general it may be presumed *that the same external influences demanded the reversion which at an earlier time called forth the formation of the Perennibranchiate stage.*

In favor of this conjecture we may adduce the experiments here communicated, for evidently it is the stimulus of the air breathing which brings the young Axolotls to the reversion to the Amblystoma form, *i. e.*, the same stimulus under whose dominating influence the Amblystoma form must have arisen.

But the case is quite similar with the season-dimorphous butterflies. There a reversion of the summer brood to the winter form is most easily called forth by the operation of cold, *i. e.*, by the same influences under whose control the winter form was developed. We know, at any rate, that reversion may arise also from the crossing of races and species, and I sought to show that reversion in butterflies may also be called forth by other influences than cold. But the most probable presumption is evidently the one that the reversion was induced through a recurrence of the same cause which to a certain extent produced the Perennibranchiate form. That this form has been shaped under the influence of life in the water admits of no doubt; and so my conjecture is that the hypothetical *Amblystoma Mexicanum*, the supposed ancestral form of the present Axolotl of the Lake of Mexico, *must have been brought to revert to the Perennibranchiate form by the circumstance that the possibility of going on land was taken from it and it was constrained to stay in the water.*

I will not reject beforehand every other opinion. We must carefully distinguish between the mere provocations which are able to produce sudden reversion and *actual causes of variation* which have for their result, directly or indirectly, the molding of a species. So it would not be inconceivable *a priori* that reversion should occur through the working of an impulse which has nothing to do with the *origin* of the phyletically older form. Certainly temperature has had no share, or only a very slight one, in the fashioning of the Perennibranchiate form. Yet cold, in and for itself, might quite well be one of the provocations which one day caused the Amblystoma form to revert to the Siredon form; and one could not *a priori* contradict DE SAUSSURE when he expresses the opinion that the low temperature of the Mexican winter must hinder the transformation (of the Axolotl to the Amblystoma) which had taken place "in the hot reptile room" of the Paris Jardin des Plantes. He supports his view by the fact that "TSCHUDI has found the Amblystoma" (of course another species) "in the hottest part of the United States." "On the plateau of Mexico, however, it snows every winter; and although the lake does not freeze, its temperature must sink very low near the surface."

But although no theoretical considerations oppose this view, yet I do not think it correct. I question very much that it was the temperature which induced the change from the Amblystoma back to the Axolotl,

or—according to DE SAUSSURE'S explanation—which at the present hinders the transformation of the Axolotl in the Lake of Mexico. This is the reason for my doubt: From all portions of the United States to the northward of New York Amblystomas have been collected; a proof that even a much greater degree of winter cold than that found on the plateau of Mexico is no hinderance for the transformation of the Axolotl; that the genus does not prove more sensitive in this respect than our native genera of *Salamandrida*.

More consideration seems to me to be deserved by the following remarks of DE SAUSSURE, in which he points out the character of the Mexican lake: "The bottom of this lake is flat, so that one comes imperceptibly from the lake to wide, swampy regions before he reaches firm ground. Perhaps this condition makes the Axolotl unable to get to the dry land, and so hinders the transformation."

At any rate the Lake of Mexico offers very peculiar conditions of life for an amphibious animal. My esteemed friend, Dr. V. FRANTZIUS, called my attention to it that this lake, like many others also of the Mexican lakes, is brackish. At the time of the conquest of Mexico by Ferdinand Cortez this circumstance caused the final surrender, as the Spaniards cut off the water from the besieged and the lake water is not drinkable. The old Mexicans had already built conduits from the distant mountains, and at the present day the city is still dependent on the water brought in by aqueducts.

Now, this saltness, in and for itself, could be no cause for the falling back to the Perennibranchiate form, but might be such a cause, in connection with other peculiarities of the lake. The shallowest part of the lake is the *eastern*, and only in this part does the Axolotl live. In the winter violent storms from the east blow regularly and persistently, which come down from the mountains and drive the water before them so powerfully that it rises in the western part of the lake and frequently causes overflows there, while from the flat eastern shore the bottom is laid completely dry for 2,000 feet.* Now if one puts together these two peculiarities, the salt and the periodical drying of a part of the lake-bottom by continued winds, he gets at any rate conditions of life for the Axolotl such as can be found in very few other places. To be sure, one might attempt to turn them to use just in an opposite sense, unfavorable to my theory, for the withdrawing of the water from a great part of the lake bottom ought—so might one think—rather to make easier the animal's transition to living on the land; yes, just compel it thereto. But one forgets, however, that the bared lake-bottom *is a sterile plain*, without food and without hiding-place; above all, without vegetation; and further, that through the pretty considerable saltness of the water (specific gravity, 1.0215) all the surface laid dry must be covered with a crust of salt, a condition which will make feeding on the land just impossible.

* Mühlenpfordt, Versuch einer getreuen Schilderung der Republik Meijco, Hanover, 1844, ii, p. 252 (Attempt at a true Picture of the Republic of Mexico).

Chloride and carbonate of soda, chiefly, are dissolved in the water in so sensible a quantity that they are regularly precipitated as a crust on the shore of the lake, and this crust is gathered there during the dry season and comes into the market under the name of tequisquite.

So, therefore, there is no lack of points of support for the conjecture that peculiar circumstances made life on the land more difficult to the animal than life in the water, and this alone might have been sufficient to bring it back to the habit of water-life only, and with that also to the reversion into the Perennibranchiate or Ichthyodea form.

Yet a truce to conjectures. We cannot lament that from the great distance and lapse of time, we are not in the condition to ascertain with definiteness the causes which compelled the Axolotl to give up the Amblystoma stage, so long as we are not able to solve the case of reversion that lies much nearer to us in the Tritons of FILIPPI and JULLIEN. Yet here, also, universal causes affecting the whole colony of Tritons must have been at the foundation, since, at least in FILIPPI'S case, the great majority of the individuals remained in the larva state. It must be that experiments with Triton larvæ would bring greater clearness here; they would have to determine, before all else, whether the reversion can be called forth artificially, and, if this is the case, through what influences.

According to the above-quoted experiences with butterflies, as well as according to the results attained with Axolotls, we should have to expect with the Tritons that the reversion to the Ichthyode form would occur if one would continue the stimulus of the water bathing the gills and the whole body, and at the same time would take away the stimulus under whose operation the *Salamandrida* form has been fashioned—the stimulus of the air bathing the gills, the skin, and the lungs. I hope at a later time to be able to report on experiments of this kind.*

No one will wish to object to my hypothesis of reversion, that on one side it opposes what it of itself postulates on the other side: *a sudden change of structure.* The characteristic of the reversion is precisely in reaching at a bound an older, that is, an earlier existing phyletic stage. That this occurs is a fact; while the reaching at a bound, to express myself figuratively, of an aim (pardon the word) that lies forward has never yet been proved or even made probable.

But as we succeeded in finding in the Axolotl's present conditions of life-forces which make its life on the land difficult or quite impossible, and therefore show a motive for that return to the Ichthyodea form which seems to have taken place; so can the other side of my hypothesis

*At any rate, SCHREIBERS seems, in his essay already cited above, to have communicated experiments from which it follows, as LEYDIG recapitulates them in the place referred to, that the last change, *i. e.*, the loss of the gills, "may be delayed by forcible means." To be sure, it does not follow from this that the animals of the experiment also became sexually mature at the same time. Unfortunately I could not myself examine the paper, as the volume of the Iris for 1833, as referred to, contains nothing of the kind, and I have lived for a long time at a distance from any large library.

be supported by facts, namely, the assumption that the ancestors of the Axolotl had at an earlier time already been Amblystomas.

We know from HUMBOLDT* that the surface of the Lake of Mexico once lay considerably higher than at present, and that in a time comparatively modern. We know, further, that the plateau of Mexico was covered with forest, while now the forest has vanished where the settlements of man, especially of the Spaniards, have reached. Now, if one may suppose that somewhere about the diluvial epoch the mountain forest extended to the edge of the lake, then still deep and with abrupt shores and containing considerably less salt, we have indicated conditions of life not only different essentially from the present ones, but also such as were quite specially favorable for the shaping of a species of the Salamandrida.

In the light of all this I believe people will not be able to cast upon my attempt to explain the exceptional metamorphosis of the Axolotl from the Lake of Mexico the reproach of being too free a flight of fancy. *At any rate it is the only possible explanation* which can be opposed to that other one which assumes that the occasional transformation of the Axolotl is not reversion, but an effort to advance. And this assumption must, in my estimation, be rejected on purely theoretical grounds by every one who thinks a *sudden* transformation of species *inconceivable, at least when it is joined with adaptations to new conditions of life.* That assumption must be rejected by every one who looks upon adaptations not as the work of magic arising at a stroke, but as the final result of a long succession of natural causes, though separately slight and imperceptible.

Should my interpretation of the facts be correct, this history of transformation would not have a significance so far-reaching as if it could have been taken in favor of heterogeneous creation, namely: in that case, demonstrating the existence of heterogeneous creation, it would have settled the question between that and transmutation. Now, on the contrary, it brings no definite decision, because, strictly taken, the refutation of sudden transformation in *one* case only proves it as not present for this *one* case.

But it is, after all, a contribution to the gradual and complete rejection of such sudden transformation. If one case after another which seemed to speak for heterogeneous creation is proved untenable on that theory, the argument by induction must finally acquire sufficient strength to be acknowledged as satisfactory.

If my view of the facts is correct, a few corollaries result from it which here at the close I should like to mention briefly.

First, a thing that is more external:

If the *Siredon Mexicanus* Shaw only assumes the Amblystoma form by occasional reversion, but never reproduces as such, but only as *Siredon*, we cannot approve the action of the latest writers on systematic zoology, who simply strike the genus *Siredon* out of the system, and

*See Mühlenpfordt's book already quoted, vol. i.

bring in the *Siredon Mexicanus* as an unwelcome addition under the genus *Amblystoma*. So long as there are not *one* only, but *several* species of *Siredon* on the earth, which are regularly reproduced *as such* and only as such, so long the genus exists. And if we would not quite rob the systematic writers of the hope that some time these species of *Siredon* would rise to be *Amblystomas*, yet it corresponds better to the state of things now existing on the earth if we still allow the genus *Siredon* to stand among the genera of fish-salamanders and reckon in it all those species which, like the Paris Axolotl, the *Siredon Mexicanus* Shaw, and proba bly also *Siredon lichenoides*, only take the Amblystoma form as an exception or by artificial influences, but without reproducing themselves in it.

On the other hand, all those species may probably be added to the genus Amblystoma which reproduce in this state, and in which the Perennibranchiate stage appears only as a larval condition.

To make this distinction in the individual case will be chiefly the task of the American naturalists, from whose ever-increasing activity we may hope indeed for fuller details on the reproduction of the numerous spe cies of *Amblystoma* in their native land. I should rejoice if my explana'ions here presented should give an impulse to such investigations.

The second corollary to which I referred is of a purely theoretical nature. It concerns an addition to the "*fundamental law in the genesis of life*," first set forth by Fritz Müller and Haeckel. It is well known that this is stated in the following proposition: The Ontogenesis contains in itself the Phylogenesis, more or less contracted, more or less modified. Although the proposition cannot be rigidly proved, because we have no means of seeing the phyletic development directly unfolded before our eyes, yet its correctness and general validity can be made so highly probable, in an indirect way, that few naturalists of the present time doubt it who have occupied themselves with the history of development and comparative morphology.

Now, according to this proposition, every stage of the phyletic development, when it is displaced by a later one, must remain included in the Ontogenesis, and therefore come to light in the form of an ontogenetic stage in the development of every individual. Now, with this my explanation of the Axolotl's transformation appears to stand in contradiction, for the Axolotl which had in former generations been an *Amblystoma* contains nothing of the *Amblystoma* in its Ontogenesis. Nevertheless the contradiction is only apparent. *As soon as a further development is actually in question*, and therefore the attainment of a new stage not yet realized, so soon the older stage is taken up into the Ontogenesis. But it is not so when the new is not actually new, but has at a former time presented the final stage of the individual development, or, in other words, when there is a *reversion*, not of the single individual, but *of the species as such* to the preceding phyletic stage, and, therefore, a phyletic sinking back of the species. *In this case the final stage of the Ontogenesis is simply eliminated, it falls out, and we can only recognize its*

presence by the fact that it may occasionally appear as a reversionary form. Thus the Triton, under some circumstances, sinks back to the Perennibranchiate stage, but not in such a way that the individual would first become a Triton and then be transformed back to a Perennibranchiate, but, as I have already made prominent above, simply by no longer reaching the stage of the *Salamandrida* and remaining upon the stage of the *Ichthyodea*. Thus, also, according to my hypothesis, the *Salamandrida* that formerly lived on the shores of the Lake of Mexico, the *Amblystoma Mexicanum*, has sunk back to the stage of the fish-salamander, and the only trace which remains to us of his former height of development is just the inclination, more or less present in every individual, to reach under favorable circumstances the salamander stage again.

But the third and last consequence which my explanation of the facts brings with it lies in the altered part which would be assigned by it to reversion in organic nature. Hitherto atavistic forms have been regarded only as isolated, exceptional cases, interesting, to be sure, in a high degree for our knowledge, but without significance for the course of development of organic nature. Now a real importance would have to be allowed them in this latter regard.

I should assume that reversion may in a twofold manner be a controlling power for the preservation or restoration of a form of life. In one case, as in the Axolotl, where the newer form, standing organically higher, becomes untenable from external causes, and now, as a further development in the other direction does not seem possible, instead of simply dying out, a reversion of the species to the older and less highly organized step follows. But, second, in this manner, *that the older phyletic form is not altogether given up*, while the younger is developed from it, *but that it alternates periodically with the younger*, as we see in the season-dimorphous butterflies. One will hardly urge any objection to it if I regard the alternation of summer and winter form in these as a periodically occurring reversion to the phyletically older form (the winter form).

Though the total reversion of a species, as I assume it for the Axolotl, may be a rarely-occurring case, the *periodically* or *cyclically occurring reversion* surely is not; it certainly plays a considerable part in the origin of various forms of the alternating or cyclical mode of reproduction.

POSTSCRIPT.

It was intimated in the foregoing discussion that the causes from which I derived the reversion of the hypothetical *Amblystoma Mexicanum* to the Axolotl of to-day, did not seem to me to suffice completely for the explanation of the phenomenon. For one thing, they appeared to me of too local a nature, as they could only be applied with certainty to the Axolotl from the lake of the Mexican capital, while also the Paris Axolotl, coming from another part of Mexico, requires an explanation that will apply to him. But, on the other hand, they did not seem to

me cogent enough. For should we even learn at a later time that the Paris Axolotl also comes from a salt lake, which is exposed to winds similar to those of the Lake of Mexico, yet there lies after all in these peculiarities of the lakes only a force which *renders difficult* the metamorphosis of the larva and the gaining of a suitable new dwelling-place on the land. The *impossibility* of attaining such a dwelling, or indeed the *total lack* of it, does not necessarily result from them.

Evidently it would be a much more substantial support for my hypothesis if I succeeded in pointing out forces in the physical relations of the country *which entirely preclude the existence of Amblystoma there.*